ALLPAHUAYO: FLORISTICS, STRUCTURE, AND DYNAMICS OF A HIGH-DIVERSITY FOREST IN AMAZONIAN PERU[1]

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Abstract

This paper describes the results of a floristic inventory at the Allpahuayo Reserve, near Iquitos in Amazonian Peru. Two long-term one-hectare plots were established using a pre-determined sampling grid, with each individual tree and liana over 10 cm diameter collected at least once, except for palms. The plots were re-censused after 5 years to quantify forest dynamics. Floristic analysis shows that the Allpahuayo forest is among the most diverse site yet inventoried, with 281 to 311 species per hectare, and at least 466 species and 61 families in the 1277-stem two-hectare sample, confirming that upper Amazonia is a world center of tree biodiversity. The ecologically most dominant and speciose family in the plots is Fabaceae sensu lato, with 231 stems and 89 species; no other family represents more than 7% of the species or 10% of the stems. In contrast to the exceptional floristic diversity, both the structure and the dynamics of the Allpahuayo forest are similar to those recorded from other old-growth neotropical forests. Many tree and liana canopy species were previously unknown to both the Iquitos area and to Amazonian Peru, which demonstrates the significance of Amazon ecological studies to systematic botany.

Resumen

Este documento describe el estado actual de los resultados de un inventario florístico a largo plazo, en la Reserva Biológica de Allpahuayo, cerca de Iquitos, en la Amazonía Peruana. Allí se establecieron dos parcelas de una hect. cada una, usando un muestreo pre-determinado, cada árbol, palmera o liana, mayores o iguales que 10 cm de diám. fué marcado y colectado, excepto las palmeras que fueron colectadas solo una vez por especie. Las parcelas fueron re-censadas despues de 5 años para cuantificar el proceso de la dinámica del bosque. El análisis de los resultados nos muestra que el bosque de Allpahuayo, está entre los bosques mas diversos hasta ahora inventariados, con 281 a 311 especies por hect., y al menos 466 especies y 61 familias en 1277 individuos en dos hect. muestreadas; éstos datos apoyan la idea de que el oeste de la Amazonía es un centro mundial de diversidad de árboles. En las parcelas la familia Fabaceae s.l., es la mas dominante ecologicamente y en número de especies, contiene 231 tallos y 89 especies; ninguna otra familia representa más que el 7 por ciento de las especies o el 10 por ciento de los tallos. En contraste a la excepcional diversidad florística, tanto la estructura del bosque como la tasa de mortalidad en Allpahuayo, están dentro los rangos de otros sitios neotropicales. El valor de los estudios ecológicos para la botánica sistemática, se demuestra en tanto que, antes de que empezáramos a tomar datos ecológicos e instalar parcelas permanentes, muchas especies de árboles y lianas eran desconocidas tanto en el área de Iquitos, como en la Amazonía Peruana.

Key words: Amazonia, floristics, inventory, Neotropics, species richness, species turnover.

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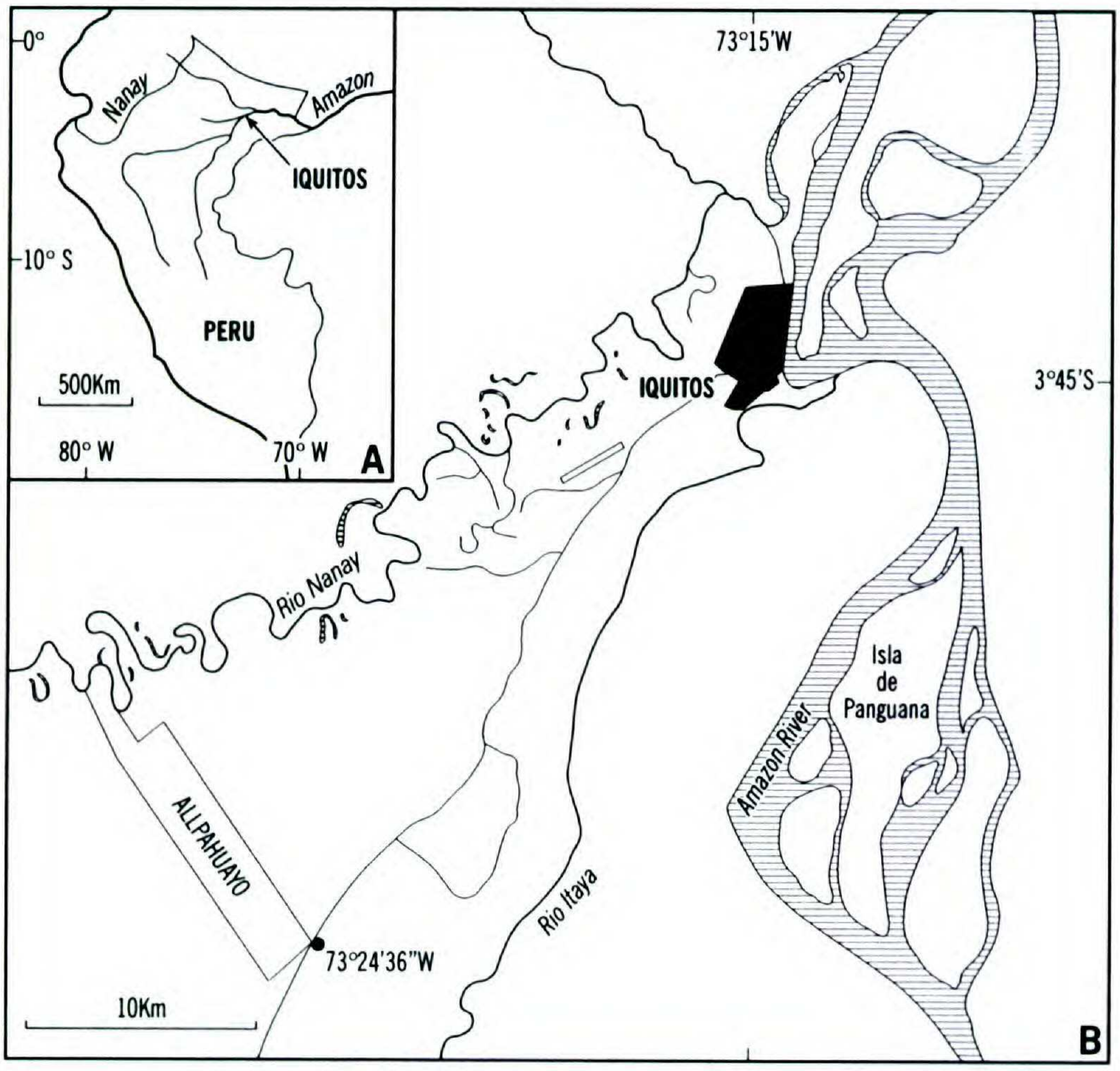

Figure 1. Map showing location of study region in relation to Iquitos and Peru. —A. Peru. —B. Iquitos region, showing location of Allpahuayo. Modified from Kalliola et al. (1998).

Biodiversity is at risk in much of the tropics. Yet biological research and conservation initiatives are hampered by inadequate baseline information. Thus, sufficient data on the numbers, kinds, and abundance of most major plant and animal taxa are not available. Moreover, knowledge of species associations and biogeographic distributions of taxa remain meager (McNeely et al., 1990; National Science Board, 1990; National Research Council, 1992; Phillips & Raven, 1996).

In the Neotropics, the extraordinary species richness, our limited taxonomic understanding, and the physical inaccessibility of most areas are formidable barriers to phytogeographic investigation. Traditional biological inventory efforts that rely mostly on ad hoc collection efforts and lengthy monograph studies cannot address the knowledge gap alone. Alternative methods are critical to improve our understanding of the factors determining species composition and the ecological dynamics of tropical forest ecosystems. In recent years there has been growing scientific interest in more ecological, plot-based work as a means of understanding tropical forests (e.g., Gentry, 1988a, b; Phillips & Gentry, 1994; Phillips et al., 1994; Dallmeier & Comiskey, 1998a, b). This approach can contribute greatly to floristic understanding by generating large numbers of new collections that are associated with site-specific ecological information. Botanical institutions play a vital role in initiating and supporting this work, and contribute essential expertise for ensuring accurate voucher determination. Equally, ecological inventories generate much biogeographical data of relevance to monographic and phylogenetic studies. Such eco-floristic research has recently been initiated in several tropical countries, including Madagascar (Lowry et al., 1997; Rakotomalaza & Messmer, 1999), Colombia (Rudas, 1996), and Peru (Gentry, 1988a, b). This paper reports the results of a similar research program at the Allpahuayo Reserve, near Iquitos in northern Peru.

Study Site

The Allpahuayo Reserve (3°57′S, 73°26′W) lies southwest of Iquitos in Amazonian Peru, between the blackwater Rio Nanay on the northwest and the Iquitos–Nauta road to the southeast (Fig. 1). This 2750-ha reserve is administered by the Peruvian Institute for Amazonian Research (IIAP). The climate is humid and hot (with the mean annual precipitation about 3000 mm and an average temper-

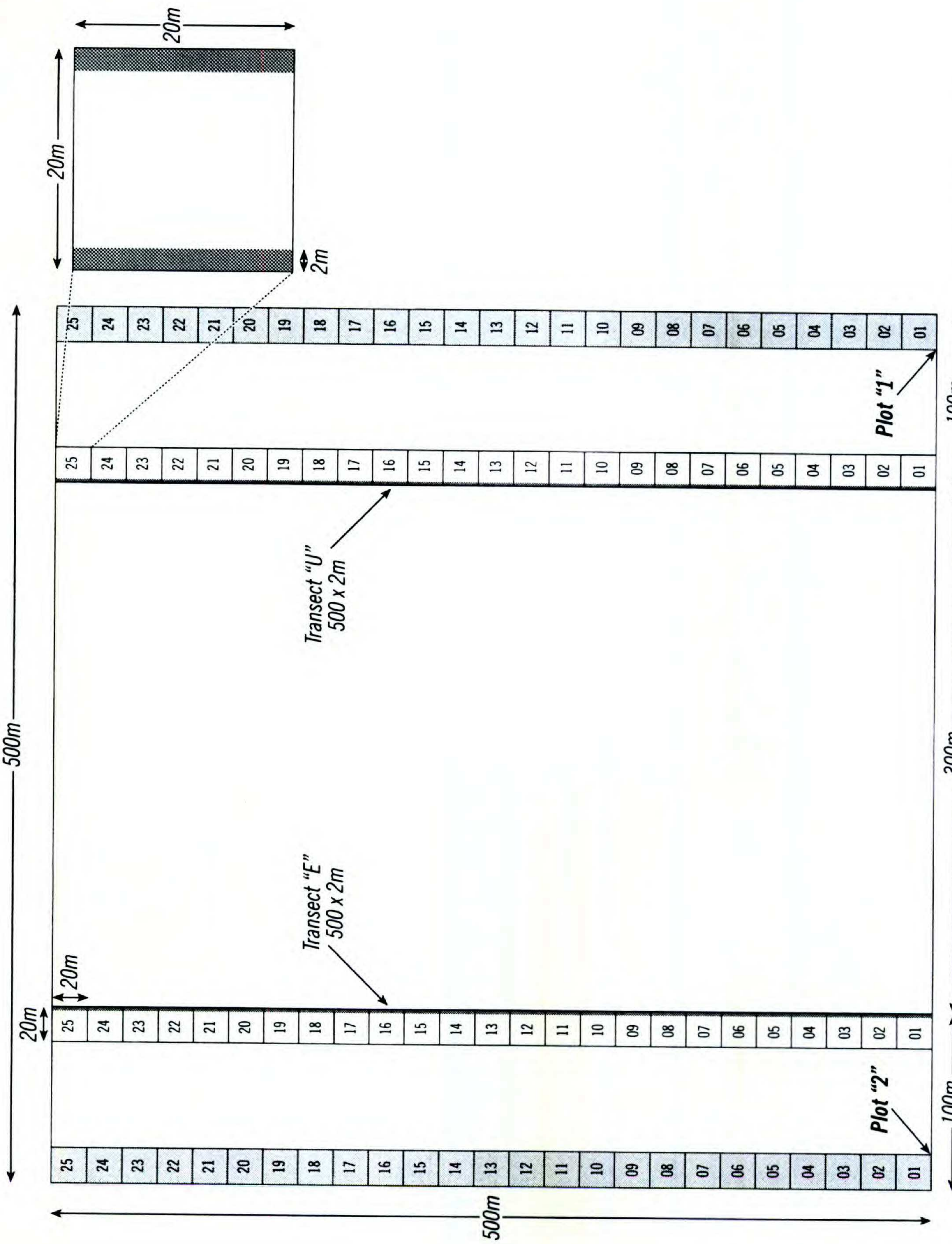

Figure 2. Diagram showing the arrangement of plots within a 500 × 500 m sampling grid at Allpahuayo. The permanent 500 × 20 m plots ("1" and "2") are located at the edges of the grid. Additional parallel temporary samples of 500 × 2 m were established 100 m in from the edges (Transects "E" and "U," shaded in the figure). For comparison we also show the relative positions of additional 500 × 20 m plots that incorporate transects "E" and "U" at other sites in Peru (Cusco Amazónico and Sucusari/ACEER) but not at Allpahuayo.

ature of 26°C; Marengo, 1998). Allpahuayo Reserve lies between 110 m and 180 m above sea level. Edaphic conditions are variable, representing a mosaic of patches ranging in texture from clayey to almost pure sand, and in drainage from waterlogged swamps to well-drained hill tops. Vegetation is mature, old-growth forest, although some palm trees (*Oenocarpus bataua* Mart.) have been cut to harvest their fruits. Allpahuayo and neighboring Mishana comprise one of three locations within 100 km of Iquitos where the Missouri Botanical Garden has been conducting a long-term floristic inventory effort with the institutional collaboration of IIAP and Explorama Tours S.A. (Vásquez, 1997). The other two sites, Reserva Ecológica Explorama Lodge (Yanamono) and Reserva Ecológica Sucusari (ACEER), have rather different soil conditions and floristic composition. The 3750 ha of Allpahuayo-Mishana is extremely species-rich, with more than 10% of the plant species reported from the whole of Peru (Brako & Zarucchi, 1993) recorded here (Vásquez, 1997).

Methods

Sampling took place within a 500 × 500 m grid in the Allpahuayo Reserve, sufficiently far from the Iquitos-Nauta road (> 2 km at its nearest point) to minimize human disturbance, yet close enough to the research station (3 km) to allow us to commute daily. Within the sampling grid, two long-term plots were established in a pre-determined location within the grid (Fig. 2) to eliminate subjective bias. Each plot is 20 × 500 m, with each plant ≥ 10 cm DBH (diameter at breast height, 1.3 m) marked with sequentially numbered aluminum tags. Additional narrower samples of 2 × 500 m with all plants ≥ 2.5 cm DBH collected but not tagged were made at pre-determined points in the grid: the results of these inventories will be reported in a future publication. The linear nature of all our plots means that they each traverse a mixture of edaphic formations. Soil conditions within the grid ranged from poorly to adequately drained clay soils ("Shapaja") to well-drained white sand soils at topographic high points ("Varillal").

In the long-term plots, every tagged plant's height was visually estimated and its diameter measured at 1.3 m with diameter tape. Herbarium collections (*Vásquez 14592–15829*) were made in 1990 and 1991 from every individual plant (except for palm tree species, which were only collected once each) using extendable aluminum collecting poles and, where necessary, spiked climbing irons for climbing trees. A full set of duplicates is deposited in two Peruvian herbaria (AMAZ, USM) and at MO, with partial collections existing at IIAP and the Universidad Agraria La Molina (MOL), as well as distributions to family specialists worldwide.

Fertile collections were made on occasion whenever flowers or fruits of plot species were seen, but in common with other tropical plot inventories most species (90%) are represented only by sterile material. At MO every collection number was first identified to family by the first author and Ron Liesner, with each family set then distributed to family specialists (Anacardiaceae, Apocynaceae, Bignoniaceae, Burseraceae, Chrysobalanaceae, Dilleniaceae, Fabaceae, Lauraceae, Lecythidaceae, Malpighiaceae, Melastomataceae, Meliaceae, Moraceae, Myrtaceae, Rubiaceae, Sabiaceae, Sapindaceae, Sapotaceae, Simaroubaceae, Violaceae). For most species at least three fertile Peruvian collections were noted for verification (MO), most deriving from the Iquitos Florula project (Vásquez, 1997).

Re-census of both plots was done in February 1996, with the re-measurement of all trees and lianas. Plants that had died in the intervening period of 5.25 years were noted as such, with evident cause of death. Each new recruit into the 10 cm DBH class was measured, tagged, and given a unique number. New recruits were collected and vouchers distributed to herbaria as for the original collections.

In order to maximize potential comparability with other forests, diversity values for each plot were expressed in terms of both species richness and Fisher's Alpha, using various subsets of our data. We estimated "species richness"—the sum of the number of tree species—as this measure is easily understood and widely reported from other forests. We also estimated Fisher's Alpha, where:

$$\text{species richness} = \text{Alpha} * \ln(1 + \text{stems}/\text{Alpha})$$

Fisher's Alpha values from small tropical forest tree samples provide good estimates of the overall diversity of each forest (Condit et al., 1998). Both species richness and Fisher's Alpha values were calculated on a per-area basis (i.e., for each one-hectare plot), and on an area-independent basis (i.e., for the first 500 stems encountered in each plot) in order to remove the complicating effect of varying stem density. Finally, each diversity index was also estimated separately for all woody stems, and for trees alone.

In order to compare stem densities of individual species and families, average per-hectare values were calculated. The most speciose families across

Table 1. Allpahuayo forest diversity in 1990, for stems ≥ 10 cm diameter in 1-ha plots. The values given for species richness and Fisher's Alpha are for the minimum and the most likely (underlined) estimates, respectively. The diversity values are calculated for (A) all woody stems (i.e., trees and lianas), and (B) for trees only. See text for further details.

	Stems	Species	Fisher's Alpha	Species per first 500 stems	Fisher's Alpha, first 500 stems
(A) All woody stems					
Plot 1	643	281/293	190/208	233/242	170/185
Plot 2	634	306/311	233/242	250/255	199/208
Plots 1 and 2 combined	1277	466/480	264/280	N/A	N/A
(B) Trees only					
Plot 1	616	264/275	175/191	228/237	162/176
Plot 2	608	290/295	218/226	243/248	186/195
Plots 1 and 2 combined	1224	433/444	239/250	N/A	N/A

our whole sample were tabulated on the basis of the total species recorded in both hectare plots. The degree of departure from randomness in species' distribution with respect to soil type was explored using a binomial test based on the relative frequency with which individuals were recorded in clay soil and sandy soil forests.

Standard measures of forest structure (density of stems and total basal area of stems ≥ 10 cm DBH) were computed for each hectare plot. Annual mortality and recruitment rates were estimated using standard procedures that use logarithmic models that assume a constant probability of mortality and recruitment through each inventory period (Phillips et al., 1994; Swaine & Lieberman, 1987), and computed separately both for woody stems and for woody basal area. Turnover rates for each period were represented by the mean of recruitment and mortality rates (Phillips, 1996).

Results and Discussion

(A) Taxon identification

Of the 1277 plants in the plots in 1991, 100% were identified to family, 1249 (97.8%) to genus, and 1168 (91.5%) to species (Appendix 1). We made 1160 collections from the two plots, of which 1053 (90%) were sterile, 22 (2%) were in bud, 33 (3%) were in flower, and 52 (5%) were in fruit. The high proportion of sterile material complicated the identification process. Near-complete identification was possible only because of the large number of fertile collections from Allpahuayo and nearby localities available for comparison at MO. For most of the unidentified species, it was possible to allocate collections to morphospecies (i.e., to allocate collections to a morphological species concept, albeit unnamed), but for a few even this was not possible.

(B) Species richness and diversity

Because of the difficulties with identification there is some uncertainty about the exact number of species in our samples. We estimated a "most likely value" for species richness ($\hat{S}$) by multiplying the number of unidentified plants per sample that could not be allocated to morphospecies (U) by the ratio of species:individuals for the plants in that sample that were identified to species or morphospecies (R), and adding this value to the number of morphospecies and species concepts actually distinguished (D).

Thus, $(\hat{S} = (U * R) + D$.

This estimate probably errs on the conservative side because the most difficult plants to identify tend to be the rarest, and therefore it is likely that the ratio of species to individuals will be greater for non-identified plants than it is for identified plants.

Diversity values for each plot and for both plots combined are presented in Table 1, with results given separately for all stems and for trees alone. These reveal that the Allpahuayo plots are some of the richest 1-ha samples ever reported. The best estimate of Fisher's Alpha for trees in our plot 2 (226) is the greatest value ever recorded for trees ≥ 10 cm DBH in 1-ha plots, comparing with 221 at Yanamono in Peru (Condit et al., 1998), 211 at Cuyabeno in Ecuador (Condit et al., 1998), and 191 in Allpahuayo plot 1 (this study), all of which are upper Amazonian sites. In terms of published results of numbers of species per 500 stems, the Allpahuayo plots are surpassed only by Yanamono (Phillips et al., 1994). There are also some published inventory results of, variously, lianas, hemiepiphytes, trees, and saplings from this part of Amazonia (e.g., Gentry, 1988a, b, 1992; Valencia et al., 1994; Clinebell et al., 1995; Duivenvoorden & Lipps, 1995). These confirm that the region's unflooded forests generally have globally exceptional levels of diversity for woody plants.

Within-community ("alpha-") diversity in neotropical forests is closely correlated with climatic conditions, with the richest forests found in the hot and aseasonal equatorial lowlands (Clinebell et al., 1995). High levels of local diversity may also be a consequence of close juxtaposition of different topographical and soil formations in western Amazonia (Tuomisto et al., 1995) with "mass-effect" processes causing species to spill over from adjacent edaphically defined communities. Each Allpahuayo plot traverses contrasting substrates, of sandy and clayey soils, which contributes to the high diversity values, as some species are apparently specialized on each particular soil type (cf. (c) below). However, the Allpahuayo plots were placed without regard to forest type, so these diversity values are presumably typical for most 1-ha patches within the Allpahuayo forest. Data are also available from one 0.1-ha sample of plants ≥ 2.5 cm DBH, purposively laid out at Allpahuayo by A. Gentry and the first author so as to only sample clay soil forest (Clinebell et al., 1995; *http://www.mobot.org/MOBOT/research/applied_research/gentry.html*). Here 275 species of trees, lianas, and hemiepiphytes were found in 401 individuals, giving a Fisher's Alpha value of 386, the highest species richness and Fisher's Alpha value of all Gentry's 227 0.1-ha samples worldwide (Phillips & Miller, in prep.).

(c) FLORISTIC COMPOSITION

The Allpahuayo forest is not only very species-rich, but also has a very low degree of dominance by any one species. The ten most common species together represent less than 20% of all stems (Table 2A). Most of the families that physically dominate the forest (Table 2B), such as Fabaceae, Myristicaceae, Euphorbiaceae, Sapotaceae, and Moraceae, do so by virtue of having many species almost all of which are present at a very low density. The palm family is atypical in that its status as the second-most stem-dense family is due mostly to the high density of one species (*Oenocarpus bataua* Mart.).

The most speciose families in our entire Allpahuayo sample (Table 2C) are the same families that dominate other Amazonian forests (Gentry, 1988a). Fabaceae are by far the most species-rich, and even when treated individually the three legume subfamilies each have about as many species as the other top-five largest families (Moraceae, Lauraceae, Annonaceae, Burseraceae).

The plots each traverse two contrasting soil types, richer clay soils (the "Shapaja" series) and poor white sand soils (the "Varillal" series), and the strong local edaphic contrasts might be expected to result in some floristic differentiation within the plots. Because of the high diversity, few species were sampled frequently enough in the two plots to allow us to test the extent to which they are habitat specialists or generalists. However, among the 56 species that were relatively common, with five or more individual plants in the two hectares, a binomial test reveals that a greater number are confined to one soil type or another than would be expected under a null model of random distribution (Table 3). This analysis reveals a large number of species that are apparent specialists on the poor white sand soils (for example, *Macrolobium microcalyx, Ocotea aciphylla, Tachigali ptycophysca*, Table 3A), and a smaller group mostly confined to the relatively rich clay soils (for example, *Leonia glycycarpa, Lindackeria paludosa, Senefeldera skutchiana*, Table 3B). Note that these results are not proof of specialization, since apparent specialists could arguably be constrained to one patch of forest by chance alone, especially if they have poor dispersal mechanisms. However, a parallel study at Allpahuayo (Vormisto et al., 2000) demonstrated that the local-scale distributional pattern of soil types is closely related to plant distributional patterns, not only for tree species but for other plant groups as well, and these spatial patterns are congruent among different groups. This research confirms that the local distributional patterns of many plants within the Allpahuayo plots are influenced by edaphic conditions. The high diversity of the Allpahuayo plots is therefore not only due to high intra-community diversity, but also derives from the contrasting edaphic conditions evident within each plot.

(d) STRUCTURE AND DYNAMICS

Although the Allpahuayo plots are exceptionally species-rich, they do not appear to be particularly remarkable in terms of their physical structure. This is indicated by the fact that both their stem density and tree basal area appear to be well within the typical ranges for most lowland Amazonian forests (Table 4). However, we could find no published

Table 2. Dominant woody plant taxa at Allpahuayo.

A. The 10 species with the highest density of stems ≥ 10 cm diameter per hectare, on average and by soil type. The two plots included 1.16 ha of clay soil forest, and 0.84 ha of sandy soil forest.

Family	Genus	Stem density	Stem density, clay soil forest	Stem density, sandy soil forest
Palmae	*Oenocarpus bataua* subsp. *bataua*	39.0	26.3	55.2
Myristicaceae	*Iryanthera ulei*	14.5	8.8	20.8
Myristicaceae	*Virola pavonis*	11.5	11.3	14.6
Euphorbiaceae	*Hevea guianensis*	10.0	1.3	18.8
Fabaceae	*Macrolobium microcalyx*	9.5	0	19.8
Annonaceae	*Diclinanona tessmannii*	7.5	0	15.6
Euphorbiaceae	*Micranda elata*	7.5	0	15.6
Euphorbiaceae	*Senefeldera skutchiana*	7.5	17.5	1.0
Apocynaceae	*Aspidosperma excelsum*	7.0	1.3	12.5
Palmae	*Astrocaryum macrocalyx*	7.0	16.3	1.0
Top 10 species		121.0	82.8	175.9
All species		638.5	637	640

B. The 10 families with the highest density of stems ≥ 10 cm diameter per hectare.

Family	Stem density
Fabaceae:	115.5
Caesalpiniaceae	53.0
Mimosaceae	23.5
Papilionaceae	36.5
Indet. Fabaceae	2.5
Palmae	61.5
Myristicaceae	59.0
Euphorbiaceae	56.5
Sapotaceae	33.0
Moraceae	30.5
Annonaceae	27.0
Lauraceae	26.5
Burseraceae	21.5
Lecythidaceae	16.0
Top 10 families	420.0
All families	638.5

C. The 10 families with the highest number of species ≥ 10 cm diameter sampled throughout our 2-ha sampled area. The values given are for the minimum and most likely (underlined) number of species per family.

Family	Total species inventoried
Fabaceae:	82/89
Caesalpiniaceae	27/29
Mimosaceae	25/28
Papilionaceae	28/29
Indet. Fabaceae	2/3
Moraceae	31/31
Lauraceae	29/29
Annonaceae	27/27
Burseraceae	23/24
Euphorbiaceae	23/23
Sapotaceae	22/23
Myristicaceae	21/21
Lecythidaceae	14/14
Myrtaceae	10/12
Top 10 families	262/273
All families	433/444

Table 3. Edaphic specialists in the Allpahuayo plots. For all species with five or more individuals, a binomial test was conducted to test the null hypothesis of random distribution with respect to soil type. The hypothesis was rejected for half the 56 species tested (* ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$)). See text for further details.

Family	Taxon	Total stems	Shapaja stems	Varillal stems	Probability of random distribution
A. Specialists on white sand ("Varillal" soils).					
Annonaceae	*Diclinanona tessmannii*	15	0	15	***
Apocynaceae	*Aspidosperma excelsum*	14	1	12	**
Bignoniaceae	*Jacaranda macrocarpa*	5	0	5	*
Euphorbiaceae	*Hevea guianensis*	20	1	18	***
Euphorbiaceae	*Micranda elata*	15	0	15	***
Fabaceae (Caes.)	*Macrolobium bifolium*	8	0	8	**
Fabaceae (Caes.)	*Macrolobium microcalyx*	19	0	19	***
Fabaceae (Caes.)	*Sclerolobium bracteosum*	5	0	5	*
Fabaceae (Caes.)	*Tachigali ptychophysca*	10	0	10	***
Fabaceae (Caes.)	*Tachigali tesmannii* cf.	13	0	13	***
Fabaceae (Pap.)	*Swartzia racemosa* var. *klugii*	11	1	10	**
Icacinaceae	*Emmotum floribundum*	5	0	5	*
Lauraceae	*Ocotea aciphylla*	8	0	8	**
Malpighiaceae	*Byrsonima stipulina*	8	0	8	**
Myristicaceae	*Iryanthera ulei*	29	7	20	*
Nyctaginaceae	*Neea floribunda*	8	1	7	*
Palmae	*Oenocarpus bataua* subsp. *bataua*	78	21	53	***
Rosaceae	*Prunus detrita* vel sp. aff.	5	0	5	*
Rubiaceae	*Ferdinandusa chlorantha*	5	0	5	*
Sapotaceae	*Chrysophyllum bombycinum*	9	0	9	**
B. Specialists on clay ("Shapaja" soils).					
Euphorbiaceae	*Conceveiba rhytidocarpa*	7	6	1	*
Euphorbiaceae	*Nealchornea yapurensis*	9	8	1	**
Euphorbiaceae	*Senefeldera skutchiana*	15	14	1	***
Flacourtiaceae	*Lindackeria paludosa*	6	5	0	*
Monimiaceae	*Siparuna decipiens*	5	5	0	*
Palmae	*Astrocaryum macrocalyx*	14	13	1	***
Palmae	*Iriartea deltoidea*	13	12	1	***
Violaceae	*Leonia glycycarpa* var. *glycycarpa*	8	6	0	*

Table 4. Stem density and basal area of some lowland Amazonian forests, for stems ≥10 cm diameter per ha. Data are from this study (Allpahuayo, 1990 census) or other sources (Mishana, Tambopata, Yanamono: Gentry, 1988b; Añangu, Jatun Sacha, Belém, San Carlos de Rio Negro: Phillips et al., 1994; Cusco Amazónico: Phillips et al., unpublished data). Stem density values are per ha. Basal area values are m^2 per ha.

Site	Tree stem density	Liana and strangler stem density	Tree basal area	Liana and strangler basal area
Belém, Brazil	572		27.7	
Jatun Sacha, Ecuador	724		30.5	
Añangu, Ecuador	734		23.1	
Allpahuayo Plot 1, Peru	616	27	26.77	0.42
Allpahuayo Plot 2, Peru	608	26	27.33	0.27
Cusco Amazonico Plot 1, Peru	489	45	25.9	
Mishana, Peru	842	16	28.7	
Tambopata Plot 1, Peru	585	17	26.9	
Yanamono, Peru	580	26	32.7	
San Carlos de Rio Negro, Venezuela	744		23.0	

Table 5. Annual rates of natural stem and basal area mortality, recruitment, and increment, for stems ≥ 10 cm diameter, between 1990 and 1996. All results are based on 0.84 ha (plot 1) and 0.96 ha (plot 2).

A. Stem dynamics.

	Annual mortality	Annual recruitment	Annual turnover (mean of loss and gain)
Plot 1: Tree stems	1.89%	1.57%	1.73%
Plot 2: Tree stems	1.84%	2.04%	1.94%
Plot 1: Liana and strangler stems	4.41%	1.89%	3.15%
Plot 2: Liana and strangler stems	4.87%	8.02%	6.44%

B. Basal area dynamics. Note that the annual gain in basal area is the sum of new recruitment into the 10 cm diameter size-class, plus the growth of pre-existing stems ≥ 10 cm diameter, and annual turnover is the mean of mortality and gain rates.

	Annual mortality	Annual recruitment	Annual gain	Annual turnover
Plot 1: Tree basal area	1.76%	0.48%	2.08%	1.92%
Plot 2: Tree basal area	2.21%	0.57%	2.32%	2.26%
Plot 1: Liana and strangler basal area	5.69%	1.03%	5.72%	5.71%
Plot 2: Liana and strangler basal area	8.29%	7.24%	8.57%	8.43%

data for liana basal area (lianas are rarely systematically censused in ecological plots, and liana basal area is even more rarely reported), so it is not possible to compare Allpahuayo with other forests in this respect. Elsewhere (Phillips et al., 1998) we reported that tree basal area values have been increasing in the majority of Amazonian plots censused since the mid-1970s, which we interpreted as being a possible effect of long-term fertilization by rising atmospheric concentrations of carbon dioxide. In this context it is interesting to note that by 1996, both plots at Allpahuayo had experienced small net increases in basal area (by 0.1% and 1.9%) over the 1990 values shown in Table 4, in spite of some illegal felling of palm trees within a few of the sub-plots. Clearly a longer census interval will be needed to confirm whether the small change in forest structure is part of a long-term trend at Allpahuayo, or simply part of a pattern of random fluctuation around a long-term stable state.

To estimate annual natural mortality and growth rates we excluded the sub-plots where palm trees were cut (Table 5). Stem turnover and basal area turnover functions measure slightly different attributes of the stand dynamics—stem turnover is concerned with population dynamics (i.e., the mean of population mortality and recruitment rates), while basal area turnover is concerned with basal area dynamics (i.e., the mean of basal area mortality and recruitment plus growth of existing trees). Over the long-term an old-growth forest would be expected to have similar values of each, and at Allpahuayo the turnover rates of tree stems and basal area both averaged close to 2% per year in the first half of the 1990s. This rate is not unusual by the standards of western Amazonian forests, but it is higher than the average turnover rate for other tropical moist forests (≈ 1.5% per year based on studies at 40 different sites; Phillips, 1996). Based on our small sample of lianas and stranglers, large climbing plants appear to turn over notably faster than trees, about 5% a year, which indicates that these organisms may have shorter canopy residence times than most trees. Whether this pattern is repeated elsewhere remains to be seen, but if faster turnover of lianas and stranglers is a general property of Amazon forests it would have implications for plot studies, most of which still ignore climbers. We may be overlooking a component of the forest that is more significant ecologically than has been appreciated.

Conclusions

Our floristic and ecological results at Allpahuayo well demonstrate the ecological and systematic benefits that can result when we concentrate our joint efforts on inventories in fixed plots. For the ecologist the benefits are clear—without the collaboration of botanists in the field and the herbarium it is impossible to characterize patterns of diversity and floristic composition in most tropical forests, let alone explore the factors that determine these. As forests become more vulnerable to widespread environmental stresses such as fragmentation and climate change (Laurance et al., 1997; Phillips, 1997), plots are also needed to monitor these impacts on biodiversity. Systematists at botanical gardens therefore offer essential expertise for understanding the biological effects of global change.

For the systematist or floristic monographer, establishing permanent sample plots can help in understanding the local flora. The precise rigor of ecological sampling forces researchers to look equally at every plant that meets pre-determined criteria. In contrast, peripatetic botanizing may catalog the weedy, common, obvious, and accessible species, while missing rarer or larger plants, especially canopy trees, lianas, and epiphytes. Rigorous plot inventories can therefore reduce the spatial, taxonomic, life-form, and even seasonal biases prevalent in herbaria (e.g., Nelson et al., 1990), especially when integrated into a larger intensive collecting effort. Thus, a comparison of taxa in Vásquez (1997) with those listed in Brako and Zarucchi (1993) shows that the intensive collecting effort in permanent plots and surrounding forest at several Iquitos sites has yielded nearly 250 taxa new to Peru. At Allpahuayo, new tree taxa have been recognized in Annonaceae (2 species; Chatrou, 1998) and in Lauraceae (3 species including a new genus; van der Werff, 1993, 1997), while the repetition of plot visits has also allowed us to collect fertile material confirming new herb and shrub taxa (e.g., Kallunki, 1994; Vásquez, 1997).

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Appendix 1. Woody plant taxa ≥10 cm DBH recorded from two 1-ha plots at Allpahuayo. All taxa are trees unless indicated as *** (liana). When a voucher is fertile, we indicate its status by the following code: bd (buds), fl (flowers), ft (fruits). See text for further discussion.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Anacardiaceae	*Tapirira peckoltiana* Engl.	2	14,608	14,614 bd				
	Tapirira retusa Ducke	1	15,185					
	Tapirira sp.	1	15,794					
Annonaceae	*Anaxagorea brevipes* Benth.	1	14,815 fl					
	Anaxagorea phaeocarpa Mart.	2	14,655 bd	14,757				
	Annona duckei Diels	1	15,614					
	Annona montana Macfad.	2	14,788	15,332				
	Annona poepipigii (Mart.) Maas & Westra	1	14,695					
	Bocageopsis mattogrossensis (R. E. Fr.) R. E. Fr.	1	15,324					
	Diclinanona tessmannii Diels	15	14,819	14,840	14,899	14,907	14,919	14,928
	Duguetia cauliflora R. E. Fr.	1	15,035 ft					
	Duguetia sp.	1	15,770					
	Fusaea longifolia (Aubl.) Saf.	2	14,764 bd	15,788 fl				
	Fusaea sp.	1	15,730					
	Guatteria elata R. E. Fr.	1	15,566					
	Guatteria megalophylla Diels	1	15,039					
	Guatteria olivacea R. E. Fr.	2	14,773	14,797 ft				
	Guatteria rugosa R. E. Fr.	1	14,943					
	Guatteria schomburgkiana Mart.	2	14,770	14,812 fl				
	Guatteria sessilis Fries	2	14,844	15,204				
	Oxandra xylopioides Diels	2	15,489 fl	15,802				
	Rollinia cuspidata Mart.	1	14,877					
	Rollinia peruviana Diels	4	14,776 fl	14,869	15,203 fl	15,671		
	Rollinia pittieri Saff.	1	14,643 fl					
	Unonopsis floribunda Diels	2	14,793	15,042				
	Unonopsis spectabilis Diels	1	15,569					
	Xylopia barbata Mart.	2	15,259	15,268				
	Xylopia benthamii R. E. Fr.	1	15,622 ft					
	Xylopia excellens R. E. Fr.	1	14,897					
	Xylopia nitida Dunal	1	15,536 bd					
	Xylopia sericea A. St.-Hil.	1	15,799 ft					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)				
Apocynaceae	*Ambelania occidentalis* Zarucchi	2	15,107 ft				
	Aspidosperma desmanthum Benth. ex Müll. Arg.	2	15,251	15,425			
	Aspidosperma excelsum Benth.	14	14,823	14,825	14,831	14,839	14,852
	Aspidosperma spruceanum Benth. ex Müll. Arg.	1	14,818				
	Aspidosperma schultesii Woodson	1	15,341				
	Couma macrocarpa Barb. Rodr.	1	15,017				
	Himatanthus succuba (Spruce ex Müll. Arg.) Woodson	1	15,676				
	Malouettia killipii Woodson	2	14,601	14,622			
	Malouettia tamaquirina var. *tamaquirina* (Aubl.) A. DC.***	1	14,882				
	Odontadenia puncticulosa (Richard) Pulle***	2	15,407	15,504			
	Parahancornia peruviana Monachin	3	14,985	15,478	15,762		
Aquifoliaceae	*Ilex andarensis* vel sp. aff. Loes.	4	14,941	15,256 fl	15,427	15,435	
Araliaceae	*Dendropanax umbellatus* (Ruiz & Pav.) Decne.	2	14,908	15,440			
	Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	1	14,858	15,009			
Bignoniaceae	*Jacaranda macrocarpa* Bureau & K. Schum.	5	14,862	14,878	14,998	15,019	15,434
	Jacaranda obtusifolia subsp. *obtusifolia* Humb. & Bonpl.	1	15,015				
	Memora cladotricha Sandwith	1	15,485				
Bombacaceae	*Eriotheca macrophylla* subsp. *sclerophylla* (Ducke) Robyns	2	15,514				
	Matisia bracteolosa Ducke	2	15,620	15,662			
	Matisia hirta Cuatrec.	1	15,060				
	Matisia malacocalyx (A. Robyns & S. Nilsson) W. S. Alverson	2	15,199	15,499			
	Matisia soegengii Cuatrec.	1	15,733				
	Pachira insignis (Sw.) Sw. ex Savigny	5	14,881	15,113	15,182	15,598	15,702
	Phragmotheca mammosa subsp. *amazonica* W. S. Alverson	1	15,513				

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Boraginaceae	*Cordia mexiana* I. M. Johnst.	1	15,135					
	Cordia nodosa Lam.	2	14,624	15,660				
Burseraceae	*Crepidospermum goudotianum* (Tul.) Triana & Planch.	2	15,607	15,653				
	Crepidospermum prancei Daly	1	15,771					
	Dacryodes peruviana (Loes.) J. F. Macbr.	1	15,766					
	Protium aracouchini (Aubl.) Marchand	1	15,500					
	Protium crassipetalum Cuatrec.	1	15,822					
	Protium divaricatum Engl.	1	15,785					
	Protium ferrugineum (Engl.) Engl.	1	15,045					
	Protium fimbriatum Swart	3	15,176	15,172	15,684			
	Protium gallosum Daly	1	14,744					
	Protium grandifolium Engl.	6	15,179	15,308	15,492	15,574	15,599	15,778
	Protium hebetatum Daly	5	14,634	14,895 fl	14,898	15,563	15,567	
	Protium macrophylla (HBK) Engl.	1	15,642					
	Protium nitidifolium Daly	2	14,787	15,760				
	Protium nodulosum Swart	1	15,650					
	Protium opacum Swart subsp. *opacum*	2	14,599	14,612	15,521	15,797		
	Protium opacum vel sp. aff. Swart	2	15,521	15,797				
	Protium subserratum (Engl.) A. DC. & C. DC.	1	14,975					
	Protium tenuifolium vel sp. aff. (Engl.) Engl.	1	15,720					
	Protium trifoliatum Engl.	1	14,724					
	Protium sp. aff. *robustum*	1	15,764					
	Protium sp.	4	15,074	15,094	15,125	15,171		
	Tetragastris panamensis (Engl.) Kuntze	1	15,136					
	Trattinickia peruviana Diels	2	14,775	15,442				
Capparidaceae	*Capparis schunkei* J. F. Macbr.	1	15,806 fl					
Caryocaraceae	*Anthodiscus klugii* Standl. ex Prance	1	15,525					
	Anthodiscus pilosus Ducke	1	15,395					
	Caryocar glabrum (Aubl.) Pers.	1	15,801					
	Caryocar harlingii Prance & Encarn.	2	14,802	15,201				
Celastraceae	*Maytenus amazonica* Mart.	1	14,843					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)		
Chrysobalanaceae	*Couepia dolichopoda* Prance	1	15,284		
	Couepia guianensis Aubl. subsp. *guianensis*	1	14,659		
	Couepia racemosa Benth. ex Hook. f.	1	14,783		
	Licania arachnoidea Fanshawe	1	14,777		
	Licania blackii Prance	1	15,080		
	Licania canescens Benoist	1	15,079		
	Licania heteromorpha var. *heteromorpha* Benth.	2	14,979	14,984	
	Parinari klugii Prance	1	15,206		
	Parinari parilis J. F. Macbr.	1	15,606		
Clusiaceae	*Caraipa punctulata* Ducke	2	14,731	14,808 fl	
	Chrysochlamys weberbaueri Engl.	1	15,488 ft		
	Clusia laxiflora (Poepp.) D. Dietr.	1	15,625		
	Moronobea coccinea Aubl.	1	15,198		
	Symphonia globulifera L. f.	1	15,800		
	Tovomita speciosa Ducke	3	14,732	15,148 ft	15,640
	Tovomita stigmatosa Planch. & Triana	4	14,656	15,659	15,693	15,765
Combretaceae	*Buchenavia amazonica* Alwan & Stace	2	15,243	15,739	
Convolvulaceae	*Dicranostyles scandens* Benth.***	1	15,093		
Dichapetalaceae	*Tapura amazonica* Poepp.	1	14,673		
	Tapura coriacea J. F. Macbr.	1	15,084		
Dilleniaceae	*Doliocarpus amazonicus* Sleumer subsp. *amazonicus****	2	15,063	15,103	
	Doliocarpus novogranatensis Kubitzki***	1	14,763		
	Pinzona coriacea Mart. & Zuccagni***	1	14,680		
Ebenaceae	*Diospyros subrotata* Hiern	1	15,561 fl		
	Lissocarpa stenocarpa Steyerm.	2	15,447	15,470	

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Elaeocarpaceae	*Sloanea durissima* Spruce ex Benth.	3	14,609	15,078	15,152			
	Sloanea floribunda Spruce ex Benth.	3	14,920	15,083	15,306			
	Sloanea guianensis (Aubl.) Benth.	2	14,888	15,631				
	Sloanea latifolia (Rich.) K. Schum.	1	15,753					
	Sloanea laxiflora Spruce ex Benth.	1	14,894 fl					
	Sloanea robusta Uittien	5	14,632	14,721	15,143	15,147	15,748	
	Sloanea sinemariensis Aubl.	1	15,307					
	Sloanea tuerckheimii Donn. Sm.	1	15,803					
	Sloanea sp.	1	15,304					
Euphorbiaceae	genus	1	14,880					
	Alchornea schomburgkii Klotzsch	1	15,593					
	Alchornea triplinervia (Spreng.) Muell. Arg.	3	14,729	14,771 ft	15,011			
	Alchorneopsis floribunda (Benth.) Muell. Arg.	1	15,302					
	Conceveiba martiana Baill.	1	15,741					
	Conceveiba rhytidocarpa Muell. Arg.	7	14,611	14,630	14,738	15,560	15,600	15,617
	Conceveiba sp. nov.	3	15,633 fl	15,690	15,757			
	Dodecostigma amazonicum Ducke	1	14,700					
	Glycidendron amazonicum Ducke	1	15,048					
	Hevea guianensis Aubl.	20	14,704	14,817	14,821	14,822	14,824	14,850
	Hevea pauciflora (Spruce ex Benth.) Muell. Arg.	6	14,667 ft	14,887 ft	15,004	15,298	15,323	15,327
	Hyeronima alchorneoides Allemao	3	14,613 bd	14,616 bd	14,681			
	Hyeronima oblonga Cuatrec.	7	14,642	14,683	14,684	14,734	14,747	15,196 fl
	Mabea maynensis Muell. Arg.	3	15,071	15,480	15,334			
	Micranda elata Muell Arg.	15	15,250 ft	15,271	15,273	15,333	15,340	15,342
	Micranda spruceana (Baill.) R. E. Schult.	11	15,005	15,026	15,047	15,065	15,275 bd	15,265 fl
	Nealchornea yapurensis Huber	9	14,794	15,575	15,592	15,618	15,673 ft	15,678
	Pera benensis Rusby	1	15,274					
	Pera bicolor (Klotzsch) Muell. Arg.	1	15,424					
	Pera leandri vel sp. aff. Baill.	1	15,647					
	Plukenetia polyadenia Muell. Arg.***	1	15,651					
	Richeria grandis Vahl	3	14,678	14,913	15,501			
	Senefeldera skutchiana Croizat	15	14,596	14,646	14,657	14,660 ft	14,662	14,663

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Fabaceae	genus	1	15,825					
	genus	1	15,681					
	genus	1	15,515					
	genus	1	15,538					
	genus	1	15,624					
Fabaceae: Caesalpinaceae	*Bauhinia guianensis* Aubl. subsp. *guianensis****	4	14,636	14,710	15,594	14,728		
	Bauhinia guianensis subsp. *kunthiana* (Vogel)***	3	14,785	14,918	14,933	15,002		
	Cynometra bauhiniifolia Benth.	4	15,551	15,573 ft	15,700 ft	15,745		
	Cynometra spruceana var. *spruceana* (Hayne) J. F. Macbr.	5	14,708	15,123	15,156	15,635	15,682	
	Dialium guianense (Aubl.) Sandwith	4	14,730	15,103A ft	15,486	15,818		
	Dimorphandra macrostachya Benth.	1	14,845					
	Hymenaea oblongifolia Huber	3	14,718	15,162	15,602			
	Macrolobium acaciifolium (Benth.) Benth.	1	14,931					
	Macrolobium angustifolium (Benth.) R. S. Cowan	2	14,689	14,837				
	Macrolobium arenarium Ducke	1	15,197					
	Macrolobium bifolium (Aubl.) Pers.	8	14,860	14,963	14,974	15,252	15,352	15,388
	Macrolobium limbatum Spruce ex Benth. var. *limbatum*	3	15,608	15,680	15,704	15,299		
	Macroloboium limbatum var. *propinquum* R. S. Cowan	1	15,299					
	Macrolobium microcalyx Ducke	19	15,244 ft	15,254	15,345	15,350	15,353	15,357
	Macrolobium sp.	1	15,301					
	Macrolobium sp.	1	15,339					
	Sclerolobium bracteosum Harms	5	15,305	15,310	15,363	15,391	15,461	
	Sclerolobium micropetalum Ducke	1	15,773					
	Sclerolobium vasquezii Pipoly	1	15,634					
	Senna sp.	1	15,564					
	Tachigali cavipes (Spruce ex Benth.) J. F. Macbr.	1	15,338 fl					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Fabaceae: Caesalpinaceae	*Tachigali chrysophylla* (Poepp.) Zarucchi & Herend.	1	14,799					
	Tachigali paniculata Aubl.	1	15,717					
	Tachigali poeppigiana Tul.	1	14,804					
	Tachigali ptychophysca Spruce ex Benth.	10	15,246	15,354	15,356	15,362	15,373	15,377
	Tachigali rusbyi Harms	1	15,611					
	Tachigali tessmannii cf. Harms	13	14,917	14,921	14,942	14,944	15,346	15,349
	Tachigali sp.	1	14,996					
	Tachigali sp.	1	15,030					
	Tachigali sp.	1	14,953					
	Tachigali sp.	1	14,957					
	Tachigali sp.	1	14,965					
	Tachigali sp.	1	14,961					
	Tachigali sp.	1	14,966					
	Tachigali sp.	1	14,856					
	Tachigali sp.	1	14,859					
	Tachigali sp.	1	14,871					
	Tachigali sp.	1	14,872					
Fabaceae: Mimosaceae	*Albizia* sp.	1	15,664					
	Enterolobium barnebeyanum Mesquita & M. F. Silva	1	15,562					
	Inga acrocephala Steud.	1	15,558					
	Inga bourgonii (Aubl.) DC.	1	15,619					
	Inga capitata Desv.	1	15,109					
	Inga coruscans Humb. & Bonpl. ex Willd.	1	14,604					
	Inga densiflora Benth.	1	14,772					
	Inga laurina (Sw.) Willd.	2	15,311	15,312				
	Inga multijuga Benth.	1	15,719					
	Inga oerstediana Benth.	1	15,559					
	Inga pezizifera Benth.	2	14,810	15,493				

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)				
Fabaceae: Mimosaceae	*Inga poeppigiana* Benth.	1	15,811				
	Inga semialata (Vell.) Mart.	1	15,537				
	Inga spectabilis var. *schimpfii* (Harms) Little	1	15,545				
	Inga velutina Willd.	1	15,698				
	Inga sp.	1	15,755				
	Inga sp.	1	15,523				
	Inga sp.	1	not collected				
	Inga sp.	1	14,598				
	Marmaroxylon basijugum (Ducke) L. Rico	4	15,024	15,776	15,792	15,804	
	Parkia igneiflora Ducke	3	14,991	15,124	15,138		
	Parkia multijuga Benth.	2	14,970	15,604			
	Parkia nitida Miq.	5	14,605	14,610	14,832	15,247	15,476
	Parkia panurensis Benth. ex H. C. Hopkins	1	voucher lost				
	Parkia velutina Benoist	2	15,260	15,335			
	Pithecellobium sp.	1	14,595				
	Pithecellobium sp.	1	14,650				
	Pithecellobium sp.	1	14,651				
	Pithecellobium sp.	1	14,692				
	Pithecellobium sp.	1	15,131				
	Pithecellobium sp.	1	15,502				
	Pithecellobium sp.	1	14,652				
	Stryphnodendron polystachyum (Miq.) Kleinhoonte	2	14,972	15,568			
	Zygia latifolia (L.) Fawcett	1	14,626				
Fabaceae: Papilionaceae	*Andira macrothyrsa* Ducke	2	15,548	15,627			
	Batesia floribunda Spruce ex Benth.	2	15,044	15,705			
	Dalbergia monetaria var. *monetaria* L. f.***	5	14,676A	14,756A	15,401	15,402	15,813
	Dalbergia riedelii (Benth.) Sandwith***	1	15,761				
	Dalbergia sp.***	1	15,064				
	Diplotropis purpurea var. *leptophylla* (Rich.) Amshoff	3	14,654	15,399	15,404		
	Dipteryx micrantha Harms	2	14,762	15,166			
	Hymenolobium nitidum Benth.	3	14,967	14,989	15,322		
	Lonchocarpus spiciflorus C. Mart. ex Benth.	1	15,375				
	Machaerium sp. cf. *multifoliatum****	1	15,498				
	Machaerium cuspidatum Kuhlm. & Hoehne***	1	15,657				

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Fabaceae: Papilionaceae	*Machaerium floribundum* var. *parviflorum* Benth.***	1	14,627					
	Machaerium kegelli Meisn.***	1	15,810					
	Machaerium multifoliatum Ducke***	3	14,600	15,294	14,988			
	Machaerium sp.***	1	15,073					
	Machaerium sp.***	1	15,025					
	Machaerium sp.***	1	15,095					
	Ormosia arborea (Vell.) Harms	1	14,937					
	Pterocarpus amazonum (C. Mart. ex Benth.) Amshoff	1	14,929					
	Pterocarpus rohrii M. Vahl.	1	15,013					
	Swartzia benthamiana Miq. var. *benthamiana*	8	14,768	15,032	15,261 fl	15,292	15,628 bd	15,812 fl
	Swartzia brachyrachis var. *peruviana* R. S. Cowan	1	15,722					
	Swartzia cardiosperma Spruce ex Benth.	4	14,784	15,151	15,257 fl	15,347		
	Swartzia laevicarpa Amshoff	1	15,116					
	Swartzia polyphylla DC.	2	15,281	15,713				
	Swartzia racemosa var. *klugii* R. S. Cowan	11	14,765 bd	14,834	14,841	14,993	14,994	15,258 fl
	Swartzia tessmannii Harms	4	14,670	14,707	14,774	15,285		
	Swartzia sp.	1	15,061					
	Swartzia sp.	1	14,875					
	Taralea oppositifolia Aubl.	3	14,874	14,940	14,977			
	Vantanea parviflora Lam.	3	15,772	15,789	15,824			
Flacourtiaceae	*Casearia acuminata* DC.	1	15,177					
	Casearia combaymensis Tul.	1	14,751					
	Casearia fasciculata (Ruiz & Pav.) Sleumer	4	14,769	15,540 ft	15,552	15,686		
	Casearia javitensis Kunth	1	14,699 ft					
	Casearia sylvestris Sw. var. *sylvestris*	1	15,508 ft					
	Casearia ulmifolia M. Vahl ex Vent.	1	15,645					
	Lindackeria paludosa (Benth.) Gilg.	6	14,691	14,693 ft	15,104	15,694	15,715 ft	15,738
	Mayna grandifolia (H. Karst.) Warb.	1	15,056					
	Tetracylacium macrophyllum Poepp.	1	15,509					
	Tetrastylidium peruvianum Sleumer	7	14,798	14,827	15,150 ft	15,528	15,595 bd	15,605
Hippocrateaceae	*Salacia* sp.***	1	15,629					
	Tontelea ovalifolia subsp. *richardii* (Miers) A. C. Sm.***	1	14,676					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Humiriaceae	*Sacoglottis ceratocarpa* Ducke	1	14,615					
	Sacoglottis sp.	1	15,511					
Icacinaceae	*Dendrobangia boliviana* Rusby	1	15,145					
	Discophora guianensis Miers	1	15,422					
	Emmotum floribundum Howard	5	14,950	14,951	15,336	15,348	15,437	
Lacistemataceae	*Lacistema aggregatum* (Bergius) Rusby	4	14,594 ft	14,597	15,531	15,736 ft		
Lauraceae	genus	1	15,547					
	genus	1	15,663					
	genus	1	15,674					
	genus	1	15,643					
	Anaueria brasiliensis Kosterm.	2	14,742	14,786				
	Aniba perutilis Hemsl.	4	14,959	15,253	15,413	15,454		
	Aniba taubertiana Mez	1	15,139 ft					
	Endlicheria citriodora van der Werff	2	14,922	14,949				
	Licaria brasiliensis (Nees) Kosterm.	1	15,496					
	Licaria canella (Meisn.) Kosterm.	2	14,838	15,768				
	Licaria sp. cf. *dolichantha* Kurz	1	15,280					
	Licaria sp. cf. *rodriguesii* Kurz	1	15,570					
	Mezilaurus opaca Kubitzki & van der Werff	2	15,746	15,759 ft				
	Nectandra acuminata (Nees) J. F. Macbr.	1	15,621					
	Nectandra globosa (Aubl.) Mez	2	15,099	15,313				
	Nectandra pearcei Mez	1	15,731					
	Ocotea aciphylla (Nees) Mez	8	15,245	15,290	15,416	15,417	15,432	15,436
	Ocotea argyrophylla Ducke	4	14,932	14,925	14,936	14,939		
	Ocotea bofo Kunth	4	15,059	15,117	15,729	15,815		
	Ocotea bracteosa (Meisn.) Mez	1	15,455					
	Ocotea leucoxylon (Sw.) Laness.	1	15,418					
	Ocotea longifolia Kunth	1	15,632 ft					
	Ocotea myriantha (Meisn.) Mez	2	14,833	15,325				
	Ocotea puberula (Rich.) Nees	2	15,370	15,361				
	Ocotea whitei Woodson	1	15,140					
	Ocotea sp.	1	15,821					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Lauraceae	*Ocotea* sp.	1	15,751					
	Persea sp. cf. *boliviensis*	1	15,467					
	Pleurothyrium vasquezii van der Werff	1	15,649					
Lecythidaceae	*Cariniana* sp. cf. *multiflora* Ducke	1	14,753					
	Eschweilera chartaceifolia S. A. Mori	3	14,750	14,906	15,112			
	Eschweilera coriacea (DC.) S. A. Mori	7	14,641	15,057	15,062	15,517	15,679	15,703
	Eschweilera gigantea (Knuth) J. F. Macbr.	1	15,721					
	Eschweilera micrantha (Berg) Miers	1	15,724					
	Eschweilera rufifolia S. A. Mori	9	14,761	14,690	15,089	15,088	15,110	15,128
	Eschweilera tessmannii Knuth	2	15,102	15,134				
	Eschweilera sp.	1	14,638					
	Eschweilera sp.	1	14,661					
	Gustavia hexapetala (Aubl.) Sm.	1	15,160					
	Gustavia longifolia Poepp. ex Berg	2	14,625	14,628				
	Lecythis pisonis aff. Cambess.	1	15,097					
	Lecythis sp. cf. *chartacea* Berg	1	15,066					
Lepidobotryaceae	*Ruptiliocarpon* sp.	3	14,820	15,543	15,740			
Linaceae	*Hebepetalum humiriifolium* (Planch.) Benth.	1	15,018	15,126				
	Raucheria punctata (Ducke) Ducke	1	15,791 ft					
Loganiaceae	*Strychnos ramentifera* Ducke***	1	15,054					
	Strychnos sandwithiana Krukoff & Barneby***	1	15,775					
Malpighiaceae	*Byrsonima cowanii* W. R. Anderson	1	15,714					
	Brysonima poeppigiana A. Juss.	2	14,809	15,001				
	Byrsonima stipulina A. Juss.	8	14,902	14,927	15,031	15,049	15,431 fl	15,448 bd
	Dicella julianii (J. F. Macbr.) W. R. Anderson***	1	15,549					
	Tetrapterys mucronata Cav.***	1	15,669					
Marcgraviaceae	*Norantea guianensis* subsp. *japurensis* Aubl.***	1	14,892 fl					
Melastomataceae	*Miconia tetragona* Cogn.	1	14,969					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Meliaceae	*Carapa procera* DC.	6	14,629	14,647	14,653	14,679	14,863	14,891
	Guarea silvatica DC.	1	15,790					
	Guarea sp.	1	14,759					
	Guarea sp.	1	14,645					
	Trichilia sp. cf. *micrantha* Benth.	3	14,780	14,813	14,893			
Menispermaceae	*Abuta grandifolia* (Mart.) Sandwith	3	15,518	15,623	15,654			
	Abuta sp.***	1	15,264					
	Abuta sp. cf. *imene****	1	15,058					
	Curarea tecunarum Barneby & Krukoff***	1	15,101					
	Telitoxicum krukovii Moldenke***	1	15,277					
	Telitoxicum minutifolium (Diels) Moldenke***	1	15,466					
	Telitoxicum peruvianum Moldenke***	1	15,282					
Monimiaceae	*Siparuna cristata* (Peopp. & Endl.) A. DC.	1	15,527					
	Siparuna cuspidata (Tul.) A. DC.	1	15,781					
	Siparuna decipiens (Tul.) A. DC.	5	14,674 bd	14,766 bd	15,505	15,565	15,597 ft	
	Siparuna guianensis Aubl.	3	14,709	14,723	14,782			
Moraceae	genus cf. *Castilla*	1	15,203A					
	Brosimum acutifolium subsp. *obovatum* (Ducke) C. C. Berg	1	15,289					
	Brosimum guianense (Aubl.) Huber	3	15,487	15,616	15,709 bd			
	Borsimum lactescens (S. Moore) C. C. Berg	1	15,630					
	Brosimum potabile Ducke	1	14,741					
	Brosimum rubescens Taub.	3	14,854	14,964	15,127			
	Brosimum utile subsp. *ovatifolium* (Kunth) Pittier	5	14,836	15,165 ft	15,184	15,554	15,571	
	Castilla ulei Warb.	1	15,652					
	Cecropia distachya Huber	3	14,725 fl	15,021	15,288			
	Cecropia engleriana Snethl.	2	15,707 fl	15,708				
	Cecropia sciadophylla Mart.	1	15,615 fl					
	Ficus amazonica (Miq.) Miq.	1	15,163					
	Ficus subapiculata (Miq.) Miq.	1	15,626					
	Helicostylis tomentosa (Poepp. & Endl.) Rusby	4	14,637	14,778	15,130	15,191		
	Maquira calophylla (Poepp. & Endl.) C. C. Berg	3	14,705	15,609	15,695			

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Moraceae	*Naucleopsis imitans* (Ducke) C. C. Berg	1	15,798					
	Naucleopsis mello-barretoi (Standl.) C. C. Berg	1	15,668					
	Naucleopsis ternstroemiiflora (Mildbr.) C. C. Berg	1	15,376					
	Naucleopsis ulei (Warb.) Ducke	1	15,716					
	Perebea glabrifolia C. C. Berg	2	14,791	15,170				
	Perebea guianensis Aubl. subsp. *guianensis*	4	14,733	14,735	14,740	15,735		
	Pourouma bicolor Mart. subsp. *bicolor*	1	15,189					
	Pourouma bicolor subsp. *scobina* (Benoist) C. C. Berg	1	15,068	15,189				
	Pourouma ferruginea Standl.	1	15,683					
	Pourouma guianensis Aubl. subsp. *guianensis*	2	14,805	15,726				
	Pourouma herrerensis C. C. Berg	1	15,085					
	Pourouma minor Benoist	1	15,532					
	Pourouma sp.	1	14,631					
	Pseudolmedia laevis (Ruiz & Pav.) J. F. Macbr.	3	14,602	14,685	15,732			
	Pseudolmedia laevigata Trécul	6	14,842	14,903 bd	14,916	14,946	15,309	15,481
	Trymatococcus amazonicus Poepp. & Endl.	2	14,698 ft	15,699				
Myristicaceae	*Campsoneura capitellata* (A. DC.) Warb.	1	15,809					
	Iryanthera crassifolia A. C. Sm.	4	15,070	15,082	15,193	15,808		
	Iryanthera elliptica Ducke	1	15,146					
	Iryanthera juruensis Warb.	13	14,618	14,640	14,712	14,748	14,800	15,503
	Iryanthera laevis Markgr.	3	14,745	14,978	15,546			
	Iryanthera lancifolia Ducke	4	14,639	14,803	15,040	15,780		
	Iryanthera macrophylla (Benth.) Warb.	7	14,706	14,760	14,889	15,330 ft	15,752	15,786
	Iryanthera paradoxa (Schwacke) Warb.	9	14,739	14,846	14,853	14,865	14,890	14,901
	Iryanthera paraensis Huber	3	14,668	15,067	15,656			
	Iryanthera polyneura Ducke	2	14,855	15,482				
	Iryanthera ulei Warb.	29	14,603	14,722	14,743	15,287 ft	15,291 ft	15,510 ft

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Myristicaceae	*Iryanthera* sp.	1	15,262					
	Iryanthera sp.	1	15,519					
	Osteophloeum platyspermum (A. DC.) Warb.	4	14,701	15,484	15,561	15,750		
	Otoba glycicarpa W. Rodr.	2	15,560	15,641				
	Virola calophylla Warb.	4	15,050	15,149	15,419 bd	15,465 ft		
	Virola divergens Ducke	1	15,823					
	Virola duckei A. C. Sm.	1	15,591					
	Virola elongata (Benth.) Warb.	2	14,767 ft	15,098				
	Virola mollisima (A. DC.) Warb.	1	15,725					
	Virola multinervia Ducke	3	14,795	15,174	15,644			
	Virola pavonis (A. DC.) A. C. Smith	23	14,619	14,649	14,669	14,682	14,789	15,272 ft
Myrsinaceae	*Cybianthus peruvianus* Miq.	1	15,016					
Myrtaceae	genus	1	15,675					
	genus	1	15,687					
	genus	1	15,390					
	genus	1	15,769					
	genus	1	14,715					
	genus	1	14,816					
	genus	1	14,857					
	genus	1	14,995					
	genus	1	15,033					
	genus	2	15,408	15,410				
	genus	1	15,400					
	genus	1	15,471					
	genus	1	voucher lost					
	Calyptranthes crebra McVaugh	1	14,956					
	Calyptranthes cuspidata DC.	1	14,971					
	Calyptranthes simulata McVaugh	1	14,954					
	Eugenia patrisii Vahl	1	15,534					
	Marliera caudata McVaugh	3	15,266	15,343	15,443			
	Marliera imperfecta McVaugh	1	14,955					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Nyctaginaceae	genus	1	15,194 ft					
	genus	1	15,557					
	genus	1	14,696					
	genus	1	voucher lost					
	Neea divaricata Poepp. & Endl.	2	14,671	15,820				
	Neea floribunda Poepp. & Endl.	8	15,383	15,387	15,412	15,415	15,430	15,439
	Neea parviflora Poepp. & Endl.	1	15,795					
	Neea spruceana Heimerl	3	15,655	15,710	15,711			
	Neea verticellata Ruiz & Pav.	1	14,737					
	Neea sp. cf. *macrophylla* Poepp. & Endl.	1	15,403					
Ochnaceae	*Cespedesia spathulata* (Ruiz & Pav.) Planch.	1	14,911	14,912				
	Ouratea sp.	1	15,248					
Olacaceae	*Aptandra tubicina* (Poepp.) Benth. ex Miers	1	15,087 ft					
	Cathedra acuminata (Benth.) Miers	2	14,909 bd	15,192				
	Minquartia guianensis Aubl.	4	14,811	15,670	15,712	15,763		
	Schoepfia lucida Pulle	1	15,603					
Opiliaceae	*Agonandra brasiliensis* Benth.	1	15,737					
	Agonandra silvatica Ducke	1	15,530					
	Agonandra sp.	1	15,807					
Palmae	*Astrocaryum chambira* Burret	6	14,801 fl					
	Astrocaryum macrocalyx Burret	14	14,592					
	Euterpe precatoria Mart.	7	14,623	14,828 ft				
	Iriartea deltoidea Ruiz & Pav.	13	14,593 fl					
	Oenocarpus bataua Mart.	78	14,633	15,020				
	Scheelea moorei Glassman	3	no voucher					
	Socratea exorrhiza (Mart.) H. Wendl.	2	14,617 ft					
Polygonaceae	*Coccoloba* sp.***	1	14,960	15,613				
	Coccoloba sp.	1	15,613					
	Moutabea sp.***	1	15,550					
Quiinaceae	*Lacunaria jenmanii* (Oliver) Ducke	1	14,864					
	Quiina obovata Tul.	3	14,687	15,142	15,167			
	Quiina sp.	1	15,749					

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Rhizophoraceae	*Cassipourea peruviana* Alston	1	15,601					
Rosaceae	*Prunus detrita* vel sp. aff. J. F. Macbr.	5	14,958	15,367	15,397	15,446	15,451	
Rubiaceae	*Alseis microarpa* Standl. & Steyerm.	1	15,661					
	Borojoa clavifora (K. Schum.) Cuatrec.	2	15,180	15,636				
	Ferdinandusa chlorantha (Wedd.) Standl.	5	15,242	15,344	15,372	15,374	15,452	
	Kotchubaea sericantha Standl.	2	14,999	15,743				
	Pagamea coriacea Spruce ex Benth.	1	15,423					
	Rudgea fissistipula Muell. Arg.	1	14,915 ft					
Rutaceae	*Zanthoxylum huberi* Waterman	1	15,090					
Sabiaceae	*Meliosma herbertii* Rolfe	2	15,283 ft	15,286				
	Ophiocaryon heterophyllum (Benth.) Urb.	2	15,497	15,541				
	Ophiocaryon klugii Barneby	3	15,610	15,646	15,696			
	Ophiocaryon manausense (W. A. Rodrigues) Barneby	1	14,978					
Sapindaceae	*Cupania diphylla* Vahl	1	15,111					
	Cupania sp.	1	14,697					
	Matayba arborescens (Aubl.) Radlk.	1	15,029 ft					
	Matayba guianensis Aubl.	1	15,828					
	Matayba sp.	3	14,935	15,000	15,023			
	Talisia japurensis Radlk.	1	15,175					
	Talisia sp.	1	15,132					
Sapotaceae	Genus cf. *Ecclinusa*	1	21,365					
	Chrysophyllum amazonicum T. D. Penn.	3	15,118	15,520	15,596			
	Chrysophyllum bombycinum T. D. Penn.	9	14,866	14,930	14,976	15,034	15,072	15,249
	Chrysophyllum cuneifolium (Rudge) A. DC.	2	15,137	15,202				
	Chrysophyllum sanguinolentum (Pierre) Baehni	4	14,814	14,848	14,997	15,053		
	Ecclinusa lanceolata (Mart. & Eichler) Pierre	4	14,807	15,012	15,326	15,328		
	Ecclinusa ramiflora Mart.	1	14,884					
	Micropholis acutangula (Ducke) Eyma	1	14,713					
	Micropholis casiquiarensis Aubrev.	4	14,675 fl	14,806	15,096	15,524		
	Micropholis egensis (A. DC.) Pierre	3	14,835 bd	14,883	15,133			

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
	Micropholis guyanensis subsp. *duckeana* (A. DC.) Pierre	4	14,938	14,986	15,409	15,590		
	Micropholis guyanensis (A. DC.) Pierre subsp. *guyanensis*	2	15,092	15,369				
	Micropholis venulosa (Mart. & Eichler) Pierre	1	15,052					
	Pouteria bangii (Rusby) T. D. Penn.	5	14,849	15,037	15,076	15,129	15,187	
	Pouteria caimito (Ruiz & Pav.) Radlk.	4	14,755	15,100	15,535	15,697		
	Pouteria cuspidata (A. DC.) Baehni	5	15,276	15,359	15,396	15,475	15,572	
	Pouteria eugeniifolia vel. sp. aff. (Pierre) Baehni	1	15,119					
	Pouteria multiflora vel sp. aff. (A. DC.) Eyma	2	14,727	15,086				
	Pouteria reticulata (Engl.) Eyma subsp. *reticulata*	1	15,723					
	Pouteria rostrata (Huber) Baehni	1	14,702					
	Pouteria subrotata Cronquist	1	14,781					
	Pouteria torta subsp. *glabra* T. D. Penn.	3	15,153	15,153	15,154	15,779		
	Pouteria torta subsp. *tuberculata* (Sleumer) T. D. Penn.	2	14,720 fl	14,746 fl				
	Pouteria sp.	1	14,790					
	Pouteria sp.	1	14,717					
Simaroubaceae	*Simaba guianensis* Aubl.	1	14,607					
	Simaba polyphylla (Cavalc.) W. Thomas	1	15,688					
	Simarouba amara Aubl.	6	14,606	14,952	15,178	15,495	15,576	15,677
Sterculiaceae	*Sterculia apeibophylla* Ducke	1	15,639					
	Sterculia pruriens (Aubl.) K. Schum.	3	14,686	15,172	15,529			
	Sterculia tessmannii Mildbraed	2	15,186	15,507				
	Sterculia sp.	1	15,144					
	Sterculia sp.	1	15,539					
	Theobroma glaucum H. Karst.	1	15,734					
	Theobroma obovatum Klotzsch ex Bernoulli	1	15,556					
	Theobroma subincanum Mart.	10	14,635	14,716	14,792	15,008	15,051	15,114

Appendix 1. Continued.

Family	Taxon and authority	No. plants in 2-ha	Vásquez collections (only the first six are listed per taxon)					
Tiliaceae	*Apeiba aspera* Aubl.	3	15,014 bd	14,752 bd	15,672 fl			
	Luehea sp.	1	14,714 fl					
	Luehea sp.	1	14,648					
	Luehea sp.	1	14,658					
	Luehea sp.	1	15,685					
	Luehea sp.	1	15,754					
Violaceae	*Leonia glycycarpa* Ruiz & Pav. var. *glycycarpa*	8	14,644	14,672	14,796	15,106	15,168	15,483
	Paypayrola sp.	1	15,205					
	Rinorea flavescens (Aubl.) Kuntze	1	15,190					
	Rinorea racemosa (Mart.) Kuntze	9	14,711	14,754	15,105	15,115	15,161 ft	15,200
	Rinorea sp.	1	15,796					
	Rinorea sp.	1	15,718 ft					
	Rinorea sp.	1	15,706					
Vochysiaceae	*Qualea paraensis* Ducke	2	15,784	15,829				
	Vochysia densifolia Spruce	1	14,666					